Mangrove or mudflat: prioritising fish habitat for conservation in a turbid tropical estuary

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Abstract

Mangrove habitats are typically the focus of conservation efforts in tropical estuaries because their structural complexity is thought to support greater biodiversity and nursery function than unvegetated habitats. However, evidence for this paradigm has been equivocal in turbid tropical estuaries where unvegetated mudflats are also highly productive. The present study compared the community composition, biodiversity, nursery-role and commercial fish biomass in two mangrove habitats and one mudflat habitat in the Gulf of Paria, Trinidad. A total of 12 705 fishes, comprising 63 species from 26 families, were sampled in mangrove creeks, seaward mangrove fringe and the subtidal margin of an intertidal mudflat from June 2014 to June 2015. The composition of the creek and mudflat communities were distinct, while the mangrove fringe community resembled the mudflat more than it did the mangrove creeks. Mean species richness (MSR), total species richness (TSR) extrapolated from species accumulation curves, and juvenile species richness (JSR) were significantly greater in the mudflat (MSR = 11.4±1.0; TSR = 75±14; JSR = 9.1±0.8) than mangrove creeks (MSR = 9.0±0.5; TSR = 49±3; JSR = 6.1±0.4) and the seaward mangrove fringe (MSR = 6.4±0.7; TSR = 58±14; JSR = 5.2±0.4). Meanwhile, Shannon Weiner diversity, juvenile fish abundance and commercial fish biomass were comparable between habitats. These findings caution against the generalisation that mangroves are the most important habitat for fishes in turbid tropical estuaries. There is now a growing body of evidence that mudflats warrant consideration as important repositories of biodiversity and nursery function for juvenile fishes.

Keywords: Biodiversity, commercial, nursery, community, juvenile, Caribbean

1. Introduction

Estuaries have the greatest economic value of all the world's ecosystems (Costanza et al. 1997), with mangroves being the most productive of estuarine habitats. Yet, mangrove-lined estuaries are in severe decline, and coastal managers and scientists are prioritising areas for conservation (Beck et al. 2001, Sheaves et al. 2015). Conservation priorities have focused on the provision of nursery habitat for coral reef fish (Nagelkerken et al. 2008) and commercial fisheries (Manson et al. 2005). However, tropical estuaries are also excellent feeding grounds for adult fish (Baker & Sheaves 2006), harbour rich and diverse communities where specialised species complete their life cycles (Blaber 2007, Elliott et al. 2007), and have economic value to subsistence and artisanal fishermen (Blaber 2013). Much of our understanding of tropical estuaries has centred on clear water habitats associated with coral reefs (Nagelkerken et al. 2008, Blaber 2013). Whereas, turbid-water estuaries of large rivers support a distinct suite of species whose ecologies are based on a different group of habitats (Blaber 2008). Here, mangroves and mudflats are prominent features, but our understanding of how these habitats compare and contrast in their biodiversity and role as nursery habitats is currently limited.

Vegetated habitats, such as mangroves and seagrasses, have often been valued above unvegetated open flats (Nagelkerken & Van der Velde 2002). The architectural complexity of mangroves helps juveniles to evade predators and offers a substrate for invertebrate prey (Laegdsgaard & Johnson 2001). However, the ebbing tide forces fish out of mangroves and into surrounding areas for substantial parts of the day, thus negating some of this value (Igulu et al. 2014). Even when mangroves are flooded, many species still migrate to feed in adjacent habitats at night or as they mature (Laegdsgaard & Johnson 1995, Hammerschlag & Serafy 2010).

47 Clearly, the resource needs of all fishes are not accommodated by mangroves. Meanwhile,
48 mudflats are productive systems in their own right, where highly digestible microphytobenthos
49 underpins an abundant and diverse food supply for fishes (MacIntyre et al. 1996, Sheaves et al.
50 2016a). There is a growing body of evidence suggesting that mudflats have been undervalued in
51 their biodiversity and nursery function (Sheridan & Hays 2003, Sheaves et al. 2016a).
52 Furthermore, in microtidal systems, where interactions between mangroves and adjacent habitats
53 are diminished (Igulu et al. 2014), each habitat may harbour distinct communities reliant on
54 specific components of habitats that are not ubiquitous. Such communities will warrant
55 individual conservation measures.
56
57 Many of the arguments used for conserving estuaries are based on the predominance of
58 commercially valuable fish (Blaber 2007). Estuarine fisheries can be divided between "within
59 mangrove" fisheries - where artisanal or subsistence fishermen target valuable adult fish; and
60 "offshore of mangrove" fisheries - which are reliant on mangroves as nursery areas for
61 commercially valuable juveniles (Blaber 2007). However, few studies have compared the role of
62 different habitats for commercially valuable species, even though juveniles of several
63 commercial species rely on mudflats rather than mangroves (Ray 2005, Tanaka et al. 2011).
64
65 Mangroves are heterogenous environments, yet studies typically target only one type of
66 mangrove habitat: e.g. submerged forest (Sheaves et al. 2016b), creeks (Giarrizzo & Krumme
67 2007), or the seaward fringe (Hindell & Jenkins 2004). Studies that addressed multiple habitats
68 have been compromised by employing different gears in the different habitats (e.g. Thayer et al.
69 1987, Robertson & Duke 1990). Spatially explicit assessment - incorporating multiple mangrove

habitat types surveyed in the same manner - will better reflect the diversity of mangrove communities and provide more meaningful comparisons with alternative habitats.

The present study compared fish communities with fyke nets in three habitats of a mangrove-lined estuary, namely, mangrove creeks, seaward mangrove fringe (hereon 'fringe') and the subtidal margin of an intertidal mudflat. We posed two questions: 1) do these habitats have similar community compositions; and 2) which habitats harbour greater fish biodiversity, nursery role for juvenile fishes, and commercial fish biomass? It was hypothesised that feeding and ontogenetic migrations between habitats would be reflected in an overlap of species composition, and that mangrove habitats would support higher biodiversity, nursery-function and commercial value compared with mudflats due to their structural complexity offering food and refuge.

2. Materials and method

2.1. Study area

The Gulf of Paria is a highly turbid and estuarine environment due to discharge from the Orinoco and Amazon rivers (Hirst 1962). The eastern margin of the gulf is impounded by the island of Trinidad and a 52.6 km^2 mangrove-dominated wetland known as the Caroni Swamp (Fig. 1). The mangrove is comprised predominantly of the species *Rhizophora mangle, Avicennia germinans* and *Laguncularia racemose* (Juman & Ramsewak 2013). A tidal range of approximately 1 m on spring tides is sufficient for mangrove creeks to remain flooded at low tide. The seaward mangrove fringe extends for 21.7 km with roots and dead vegetation providing potential habitat for fish. The swamp is bordered to the north by the Caroni River which empties the largest watershed in Trinidad and forms an intertidal mudflat at its mouth. All habitats have a soft mud

93 substrate. A part of the mudflat and mangrove has been designated as a RAMSAR site of
94 international importance but the fish communities are poorly characterised in the mangrove and
95 uncharacterised in the mudflat.
96
97 *2.2. Study design*
98 For open habitats, i.e. the mangrove fringe and mudflat, the only prerequisite for site selection
99 was 1.5-3 m depths at high spring tide to accommodate the minimum fishable depth of the nets
100 and to prevent fish passing above the net. As such, the mudflat was sampled along its deeper,
101 subtidal edges. The closest mudflat site was approximately 400 m from the mangrove, while
102 fringe sites were within 10 m of the mangrove. Additional criteria were required to maintain
103 consistency and sampling efficiency across mangrove creek sites: 1) similar current; 2) creek
104 width did not exceed the width of the net (i.e. 8-10 m); 3) no obstructions to access or net
105 deployment; and 4) nets were obscured from passing boats. Few locations met these criteria and
106 creek site selection was limited to the sites used in this study. Due to differences in area of the
107 three habitats, an unbalanced design was adopted to encompass spatial variation within habitats:
108 12 creek sites, two fringe sites and two mudflat sites (Fig. 1). Sites were sampled around spring
109 tides on at least three occasions in both the dry season (June 2014, May and June 2015) and the
110 wet season (August, October and December 2014). Early June sampling targeted the very end of
111 the dry season. Strong tides caused the nets to fail on three occasions in the creeks. Hence, the
112 number of successful fyke net deployments was 69 in the creeks, 17 in the fringe and 14 in the
113 mudflat.
114
115 *2.3. Field sampling*

Fyke nets were custom modified with three 3×8 m wings (1.6 cm mesh), and a 1.1 m diameter, 5-hoop cod end (1.25 cm mesh). One net was set concurrently in each of two sites (> 1 km apart to maintain independence) from a boat at low tide and orientated to catch fish with the rising tide. Nets were deployed for 24 hrs but emptied at sunset to minimise escapes and consumption by trapped predators. Stomach contents of trapped predators were checked for prey but predation was largely limited to *Batrachoides surinamensis* and infrequent. Specimens were processed in the field whenever possible or otherwise in the lab. Specimens were identified to species level before measuring standard length (mm) and wet weight (g). Juveniles were defined based on literature values of size at maturity, and commercial species identified from dialogue with fisherman, grey literature on Trinidad and Tobago's fisheries, FAO reports and peer-reviewed literature from the wider area (e.g. Chan A Shing 2002, Mangal 2008, Mohammed et al. 2011, IMA 2016). Only species that are commercially valuable in Trinidad and Tobago or the central western Atlantic were designated as such. Physiochemical parameters (salinity, water temperature, dissolved O_2 and turbidity) were assessed midwater at each site using a YSI multiparameter probe and a secchi disk before setting and emptying the nets.

2.4. Data analysis

All statistical analyses were performed using the R statistical software (R-Core-Team 2018). PERMANOVAs tested for significant differences in community composition (by abundance) between habitats, seasons and their interaction, followed by pairwise PERMANOVAs for each habitat combination. Rare species (fewer than three individuals) were removed to focus differences on regular habitat users. Heteroscedastic variances were diminished with a log(x+1) transformation, but still remained. Therefore, differences in community composition were substantiated with non-metric multidimensional scaling (NMDS) based on a Bray-Curtis

dissimilarity matrix in the metaMDS function of the Vegan package (Oksanen et al. 2019). SIMPER analysis identified the most important species contributing to differences in log(x+1) transformed community compositions. Species accumulation curves were extrapolated to 10 000 individuals sampled (aligning sampling across the three habitats) to estimate total species richness in the package iNext (Hsieh et al. 2019). This sampling effort was a good reflection of the empirically measured species richness in the creeks. Species richness, Shannon Weiner diversity, juvenile fish abundance, juvenile species richness and commercial fish biomass were standardised per catch and square-root (richness) or log transformed (abundance and biomass) to meet assumptions of two-way ANOVAs (habitat and season as orthogonal fixed factors) and post-hoc pairwise t-tests for significant effects (Holm-Bonferroni's correction). Physiochemical parameters were compared between seasons for each habitat and between habitats with one-way ANOVAs (log and square-root transformations), Welch's t-tests for data with unequal variances and Kruskal-Wallis tests where data did not meet assumptions of the model. Temperature and dissolved O_2 were not significantly different between seasons for any habitat and so data were pooled across seasons for these two parameters.

3. Results

3.1. Community composition

A total of 12 705 fishes were sampled in the mangrove creeks (9258; no. of catches = 69) mangrove fringe (1135; n = 17) and subtidal mudflat (2311; n = 14) of the Gulf of Paria between June 2014 and June 2015. Fish community compositions were significantly different between habitats ($p < 0.001$) and seasons ($p < 0.01$), with pairwise tests showing that each habitat was distinct from the others (Table 1). However, the fringe community was more similar to the

mudflat community than it was to the creek community (Fig. 2). Communities were largely distinguished by the relative importance of *Diapterus rhombeus, Bairdiella ronchus, Centropomus ensiferus* and *Sciades herzbergii* (Table 2). *D. rhombeus, C. ensiferus* and *S. herzbergii* accounted for 61% of total abundance in the creeks (Supplement), whereas *B. ronchus* alone accounted for 67% of total abundance in the mudflat. Dominant species in the fringe overlapped with the creeks and the mudflat, i.e. *B. ronchus, C. ensiferus* and *D. rhombeus* together comprised 73% of total abundance.

3.2. Biodiversity

Field sampling recorded 63 species from 26 families, with 48 species in the creeks, 31 species in the fringe and 42 species in the mudflat (Supplement S1). Of these, 21 species were observed in all three habitats and 24 rare species were represented by just one or two individuals. Species accumulation curves, extrapolated to 10 000 individuals sampled, attained 49±3 (±1 SD) species in the creeks, 58±18 species in the fringe, and 75±14 species in the mudflat (Fig. 3). Mean species richness per catch was higher in the creeks than the fringe ($p < 0.05$), but the mudflat supported greater species richness than both the creeks ($p < 0.05$) and the fringe ($p < 0.01$; Table 3 & Fig. 4). In contrast, species diversity was not significantly different between any habitat ($p > 0.05$).

3.3. Nursery value

Juveniles accounted for 73% of all individuals in the creeks, 97% in the fringe and 91% in the mudflat. Juvenile abundance was 2.8-fold higher in the mudflat than the creeks in the wet season (Fig. 4), largely due to abundant *B. ronchus.* However, juvenile abundance per catch was not

significantly different between habitats ($p > 0.1$; Table 3). Juvenile stages were identified for 42 species, 10 of which were common as adults and thus deemed to not use the habitats specifically as nursery grounds (see Beck et al. 2001). Still, the creeks were a nursery habitat for 27 species, the fringe for 18 species and the mudflat for 21 species. Mean juvenile species richness was significantly higher in the mudflat than both the creeks ($p < 0.01$) and the fringe ($p < 0.01$; Table 3).

3.4. Commercial biomass

In the creeks, 91% of fish were commercially valuable, 94% in the fringe and 84% in the mudflat. The commercial species *S. herzbergii*, *B. ronchus*, *B. surinamensis*, *C. ensiferus* and *C. spixii* were generally the most important across habitats (Supplement S1). The average catch of commercial biomass was 5.2-fold higher in the creeks than the fringe ($p < 0.01$; Table 3 & Fig. 4). However, commercial biomass varied considerably between creeks, ranging from 2.1±0.5 kg per catch at the most landward creeks to 14.4±5.1 kg in creeks where the catfish *S. herzbergii* were particularly abundant. Mudflat sites were at the lower end of this range (2.8±0.6 kg), and differences between mudflat and creeks were not significant ($p > 0.1$). The mudflat did support a 2.4-fold greater biomass of commercial fish than the fringe, but differences were not significant ($p > 0.05$).

3.5. Physiochemical environment

All physiochemical characteristics had the greatest range across mangrove creeks which spanned 10 km from sea to land (Table 4). Temperature and DO were not significantly different between seasons for any habitat (Supplement S2), and so seasonal data were pooled for these two

variables. Mangrove creek and fringe habitats exhibited salinities close to seawater in the dry season, while lower salinity in the mudflat was due to freshwater input from the Caroni River ($F_{df=2,21} = 49.1$, $p < 0.001$). Salinities declined in all habitats in the wet season - particularly in the creeks and fringe - rendering them similar across habitats ($\chi^2_{df=2} = 3.8$, $p > 0.1$). Temperature was not significantly different between habitats (Welch's test $F_{2,37} = 0.59$, $p > 0.1$), however, DO was significantly lower in the creeks than the other habitats ($F_{2,120} = 39.6$, $p < 0.001$), averaging 2.9±0.2 mg l^{-1} in both seasons, but dropping below 1 mg l^{-1} on several occasions. Turbidity in the mudflat was diminished by the outflow of the Caroni River in the dry season ($F_{2,20} = 15.5$, $p < 0.001$), but the creeks and fringe declined to similar levels in the wet season ($F_{2,40} = 0.04$, $p > 0.1$).

4. Discussion

4.1. Habitat conservation priorities

Mangrove-lined estuaries represent one of the world's most productive ecosystems but they are also one of the most threatened (Valiela et al. 2001). Spatial conservation planning in these systems has to balance the demands of multiple users, and as such, must prioritise areas with the greatest conservation value (Beck et al. 2001). Our findings showed that subtidal mudflat can support comparable species diversity and juvenile fish abundance to two types of mangrove habitat, and even surpass their species richness of the whole community, and, more specifically, of the juvenile fish community. Mangrove creek, mangrove fringe and mudflat habitats also harboured distinct community compositions, thus warranting separate consideration in conservation planning. These communities may be less inclined to mix as fish have access to creeks throughout the tidal cycle, rather than being forced into surrounding habitats in more

232 tidally-governed systems (Igulu et al. 2014). However, commercial fish biomass was markedly
233 higher in the mangrove creeks than the other two habitats, largely due to the predominance of the
234 catfish *Sciades herzbergii* in the creeks.
235
236 Extrapolation of species accumulation curves showed that the 48 species recorded in mangrove
237 creeks of the Caroni Swamp was a good reflection of the total species richness for this habitat.
238 Comparable observations of 34, 40, 49, 65 and 70 species have been made in Brazilian estuaries
239 much larger than the Caroni Swamp (see meta-analysis in Giarrizzo & Krumme 2008). In
240 contrast, the species richness of the mudflat (42) was almost certainly an underestimate due to
241 insufficient sampling, and the extrapolated estimate may surpass 75 species. While this
242 extrapolation has large potential errors without further sampling, these estimates for total species
243 richness align with 80 species observed in a Brazilian tidal flat (da Silva et al. 2018), and
244 extrapolations of 45-90 species for upper subtidal communities in four Brazilian estuaries (Vilar
245 et al. 2013), but falls short of the 133 species reported in tidal sandflats (Spach et al. 2004).
246 Higher species richness per catch and juvenile species richness per catch in the mudflat relative
247 to the two mangrove habitats also supports the importance of the mudflat for biodiversity and
248 juvenile fishes. Previous studies have reported fish abundance and diversity to be greater in
249 mangroves compared to unvegetated flats (Robertson & Duke 1987, Chong et al. 1990,
250 Laegdsgaard & Johnson 1995), relatively similar (Hindell & Jenkins 2004, Tse et al. 2008, Payne
251 & Gillanders 2009), or superior in mudflats relative to mangroves (Blaber et al. 1989). However,
252 these studies either 1) do not use the same fishing gears in all habitats (Robertson & Duke 1987,
253 Blaber et al. 1989, Chong et al. 1990); or 2) sample the pneumatophore zone of the seaward
254 fringe (Robertson & Duke 1987, Laegdsgaard & Johnson 1995, Hindell & Jenkins 2004, Tse et

al. 2008, Payne & Gillanders 2009). Employing different gears can cause considerable sampling bias (Smith & Hindell 2005, Wang et al. 2009), and our findings support previous assertions that the mangrove fringe community may reflect open water habitats more than the mangrove forest (Huxham et al. 2004). Studies that avoided these shortcomings reported findings similar to the present study. Fish abundance was comparable in mangrove creek and mudflat habitats (Wang et al. 2009), and species richness was superior in mudflats and open areas compared to submerged forest (Sheridan 1992, Huxham et al. 2004, Wang et al. 2009).

Given the number of sub-habitats that were omitted in this study, particularly in the mangroves, it would be presumptive to conclude that, as a whole, the mudflat supports greater species richness than the mangroves in this study area, and thus should be prioritised over mangroves in fish conservation agendas. It is also important to qualify here that this study assessed the relative nursery 'potential' of mangrove and mudflat habitats based on juvenile fish abundance and juvenile species richness. Identifying valuable nursery habitats ultimately requires determining the relative contributions of recruits from all habitats to adult populations (Dahlgren et al. 2006). Nevertheless, our findings add to an accumulating body of evidence challenging the perception that mangroves are always the habitat with the greatest biodiversity and nursery value within the seascape (Sheridan 1992, Huxham et al. 2004, Wang et al. 2009). Mangroves are thought to harbour more abundant and diverse fish communities, and support a greater nursery role than unvegetated habitats because they offer superior feeding and refuge resources (Laegdsgaard & Johnson 2001). Clearly, there is sufficient ambiguity in the relative biodiversity and nursery function of habitats in turbid tropical estuaries to revisit whether these hypotheses are applicable in such systems.

278

279 *4.2. Feeding and refuge hypotheses*

280 Comparisons of food resources and their effect on growth rates in mangroves and mudflats are
281 sparse (Sheridan & Hays 2003, Lee 2008, Sheaves et al. 2016a), while comparisons of gut
282 fullness have been inconsistent across species and sizes (Laegdsgaard & Johnson 2001, Tse et al.
283 2008). Most fish in the present study were juvenile benthic invertivores - particularly favouring
284 microcrustaceans (Marley unpublished). While microcrustaceans are abundant components of
285 the epibiota of prop roots (Silva-Camacho et al. 2017), their density and diversity in mangrove
286 sediments are compromised by the poor digestibility of mangrove leaves and anoxic conditions
287 (Sheridan 1997, Dittmann 2001). In contrast, macroinvertebrate abundances peak in the
288 sediments of the lower intertidal area in front of mangroves, and this could be a critical hotspot
289 in ecological processes of tropical estuaries (Sheaves et al. 2016a). The fact that many species
290 make perilous migrations from mangroves to feed in surrounding habitats would suggest that
291 mangrove prey are inadequate (Sheaves 2005, Ley & Halliday 2007, Hammerschlag & Serafy
292 2010). Such species presumably use mangroves for refuge rather than feeding (Laegdsgaard &
293 Johnson 2001).

294

295 The predator-refuge hypothesis has been widely used to promote the nursery value of mangrove
296 habitats (see review in Whitfield 2017), even though not all mangroves provide the same level of
297 protection (Rönnbäck et al. 1999, Chittaro et al. 2005). Moreover, the shallow, turbid waters of
298 estuarine mudflats also provide protection from predators (Abrahams & Kattenfeld 1997,
299 Paterson & Whitfield 2000), and the predator-refuge hypothesis may not favour mangroves when
300 they are adjacent to other potential nursery habitats (Huxham et al. 2004, Smith & Hindell 2005).

The premise that mangroves have fewer predators has also been refuted (Baker & Sheaves 2006, Dorenbosch et al. 2009). In the present study, piscivores, such as *Centropomus* spp. and *B. surinamensis*, were more abundant in mangrove creeks than the mudflat. However, large transient piscivores, such as lutjanids, serranids and *Megalops atlanticus*, were likely to be underestimated by the size-selective fyke nets, and it is unclear what effect these predators have on prey fish assemblages.

4.4. Physiochemical environment

Abiotic conditions are some of the most important structuring forces in tropical estuaries (Nagelkerken et al. 2008). Conditions in the three focal habitats were relatively similar. Salinities were generally close to seawater, turbidity was low, and temperatures averaged 27-28°C. However, DO was significantly lower in the creeks than the other habitats. Mean DO concentrations in this study were around half of those reported in mangrove creeks elsewhere (Giarrizzo & Krumme 2007, Shervette et al. 2007), and extreme lows (<1 mg l^{-1}) could have been fatal to fish (Shimps et al. 2005). DO influences fish community composition in tropical estuaries (Vaslet et al. 2010), and potentially exerts a stronger influence on Caribbean mangrove fish communities than salinity (Bouchereau et al. 2008). DO also affects the distribution of taxa that were important components of the Caroni Swamp community: Gerreidae (Ramos et al. 2016), Ariidae (Dantas et al. 2012) and *Epinephelus itajara* (Koenig et al. 2007). More accurate assessments of DO concentrations throughout the tidal cycle, rather than the snapshot measurements of this study, are required to fully evaluate its structuring influence. Nonetheless, it has the potential to structure fish communities and be a limiting factor for many species in our

mangrove creeks. In contrast, the ability of Ariidae to tolerate low DO levels (Dantas et al. 2010) explains their high biomass in mangrove creeks and the greater commercial value of this habitat.

4.3. Sampling effects

Fish community surveys can be considered qualitative when the sampling volume of water, and thus fish densities, are not calculated (Sheridan & Hays 2003). Sampling volume could not be calculated with the fyke net method used in this study. However, sampling volume was likely to be largest in mangrove creeks where water funnelled into the forest on the rising tide, and weakest in the fringe which was far from any major channels. The nets would have also been most effective in mangrove creeks where they closed-off the channel - preventing fish from navigating around the net. As such, sampling artefacts fail to explain the relatively high abundance and species richness found in the mudflat. On the contrary, the mudflat community may have been underestimated. In contrast, the depauperate communities observed in the mangrove fringe may be better explained by sampling artefacts since other studies have documented more abundant and diverse assemblages in this habitat (Hindell & Jenkins 2004, Bouchereau et al. 2008). Deploying nets parallel to the forest edge in the fringe may have been more successful, but would have been inconsistent with sampling in the other habitats.

4.5. Seascape connectivity

Although this study has assessed three estuarine habitats in a relatively isolated manner, their ecologies are surely entwined within a mosaic of interconnected coastal habitats (Sheaves et al. 2015). Mangroves enhance fish abundance and diversity in adjacent habitats (Dorenbosch et al. 2005, Jelbart et al. 2007), mudflats serve as low tide feeding areas when the mangrove is inaccessible (Sheaves 2005), and as intermediate habitats for juveniles migrating from

mangroves to offshore adult habitats (Laegdsgaard & Johnson 1995), and adjacent habitats exchange organic matter (Marley et al. 2019). The Gerreidae, Centropomidae, and Sciaenidae were almost entirely represented by juveniles in this study area, and are known to use these habitats as nurseries in other systems and then ontogenetically migrate offshore (Chaves 1995, Aliaume et al. 1997, Chaves & Otto 1998, Chaves & Bouchereau 2000). However, studies of seascape nurseries and habitat shifts in turbid tropical estuaries have been limited to only small proportions of fish communities in Brazil (Dantas et al. 2012) and the Gulf of Mexico (Mohan & Walther 2018). As such, there are huge gaps in our understanding of how different species use tropical estuarine habitats during their lifecycles, despite this information being crucial to guide spatial conservation planning.

Conclusion

Tropical estuaries are the focus of intense modification, exploitation and pollution. In spatial conservation planning, some habitats are prioritised while others are effectively sacrificed. This study adds to the growing body of literature challenging the paradigm that mangroves are the only priority habitat for conservation in turbid tropical estuaries. Our findings emphasise the potential role of mudflats as nursery habitats, biodiversity hotspots and as critical components of ecological systems, and that their loss will have wide-ranging consequences. Therefore, it is vital that we abandon the preconception that vegetated habitats are the only priority in estuary conservation, and adopt a more integrated seascape perspective that focuses on the habitat mosaic and the interactions between habitats.

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References

Abrahams M.V., Kattenfeld M.G. (1997) The role of turbidity as a constraint on predator-prey interactions in aquatic environments. Behavioral Ecology and Sociobiology 40, 169-174

Aliaume C., Zerbi A., Miller J.M. (1997) Nursery habitat and diet of juvenile Centropomus species in Puerto Rico estuaries. Gulf of Mexico Science 15, 3

Baker R., Sheaves M. (2006) Visual surveys reveal high densities of large piscivores in shallow estuarine nurseries. Marine Ecology Progress Series 323, 75-82

Beck M.W., Heck Jr K.L., Able K.W., Childers D.L., Eggleston D.B., Gillanders B.M., Halpern B., Hays C.G., Hoshino K., Minello T.J. (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. Bioscience 51, 633-641

Blaber S.J.M., Brewer D.T., Salini J.P. (1989) Species composition and biomasses of fishes in different habitats of a tropical Northern Australian estuary: their occurrence in the adjoining sea and estuarine dependence. Estuarine, Coastal and Shelf Science 29, 509-531

Blaber S.J.M. (2007) Mangroves and fishes: issues of diversity, dependence, and dogma. Bulletin of Marine Science 80, 457-472

393 Blaber S.J.M. (2008) Tropical estuarine fishes: ecology, exploration and conservation, Vol 1.
394 John Wiley & Sons, Oxford, England
395 Blaber S.J.M. (2013) Fishes and fisheries in tropical estuaries: the last 10 years. Estuarine,
396 Coastal and Shelf Science 135, 57-65
397 Bouchereau J.-L., Chaves P.d.T.d.C., Monti D. (2008) Factors structuring the ichthyofauna
398 assemblage in a mangrove lagoon (Guadeloupe, French West Indies). Journal of Coastal
399 Research 244, 969-982
400 Chan A Shing C. (2002) Atlas – Marine fisheries of Trinidad and Tobago, part 1, Trinidad
401 inshore fisheries. Ministry of Agriculture Land and Marine Resources, Port of Spain,
402 Trinidad
403 Chaves P.d.T.d.C. (1995) Atividade reprodutiva de *Bairdiella ronchus* (Cuvier) (Pisces,
404 Sciaenidae) na Baía de Guaratuba, Paraná, Brasil. Revista Brasileira de Zoologia 12, 759-
405 766
406 Chaves P.d.T.d.C., Otto G. (1998) Aspectos biológicos de *Diapterus rhombeus*
407 (Cuvier)(Teleostei, Gerreidae) na Baía de Guaratuba, Paraná, Brasil. Revista Brasileira de
408 Zoologia 15, 289-295
409 Chaves P.d.T.d.C., Bouchereau J.-L. (2000) Use of mangrove habitat for reproductive activity by
410 the fish assemblage in the Guaratuba Bay, Brazil. Oceanologica Acta 23, 273-280
411 Chittaro P.M., Usseglio P., Sale P.F. (2005) Variation in fish density, assemblage composition
412 and relative rates of predation among mangrove, seagrass and coral reef habitats.
413 Environmental Biology of Fishes 72, 175-187

414 Chong V.C., Sasekumar A., Leh M.U.C., D'cruz R. (1990) The fish and prawn communities of a
415 Malaysian coastal mangrove system, with comparisons to adjacent mud flats and inshore
416 waters. Estuarine, Coastal and Shelf Science 31, 703-722
417 Costanza R., d'Arge R., De Groot R., Farber S., Grasso M., Hannon B., Limburg K., Naeem S.,
418 Oneill R.V., Paruelo J., Raskin R.G., Sutton P., van den Belt M. (1997) The value of the
419 world's ecosystem services and natural capital. Nature 387, 253-260
420 da Silva R.S., Baeta A.S.B.V., Pessanha A.L.M. (2018) Are vegetated areas more attractive for
421 juvenile fish in estuaries? A comparison in a tropical estuary. Environmental Biology of
422 Fishes 101, 1-16
423 Dahlgren C.P., Kellison G., Adams A.J., Gillanders B.M., Kendall M.S., Layman C.A., Ley J.A.,
424 Nagelkerken I., Serafy J.E. (2006) Marine nurseries and effective juvenile habitats: concepts
425 and applications. Marine Ecology Progress Series 312, 291-295
426 Dantas D.V., Barletta M., Costa M.F., Barbosa-Cintra S.C.T., Possatto F.E., Ramos J.A.A., Lima
427 A.R.A., Saint-Paul U. (2010) Movement patterns of catfishes (Ariidae) in a tropical semi-
428 arid estuary. Journal of Fish Biology 76, 2540-2557
429 Dantas D.V., Barletta M., Lima A.R.A., Ramos J.d.A.A., Da Costa M.F., Saint-Paul U. (2012)
430 Nursery habitat shifts in an estuarine ecosystem: patterns of use by sympatric catfish species.
431 Estuaries and Coasts 35, 587-602
432 Dittmann S. (2001) Abundance and distribution of small infauna in mangroves of Missionary
433 Bay, North Queensland, Australia. Revista de Biologia Tropical 49, 535-544
434 Dorenbosch M., Grol M.G.G., Christianen M.J.A., Nagelkerken I., Van Der Velde G. (2005)
435 Indo-Pacific seagrass beds and mangroves contribute to fish density and diversity on
436 adjacent coral reefs. Marine Ecology Progress Series 302, 63-76

437 Dorenbosch M., Grol M.G.G., de Groene A., van der Velde G., Nagelkerken I. (2009) Piscivore
438 assemblages and predation pressure affect relative safety of some back-reef habitats for
439 juvenile fish in a Caribbean bay. Marine Ecology Progress Series 379, 181-196
440 Elliott M., Whitfield A.K., Potter I.C., Blaber S.J.M., Cyrus D.P., Nordlie F.G., Harrison T.D.
441 (2007) The guild approach to categorizing estuarine fish assemblages: a global review. Fish
442 and Fisheries 8, 241-268
443 Giarrizzo T., Krumme U. (2007) Spatial differences and seasonal cyclicity in the intertidal fish
444 fauna from four mangrove creeks in a salinity zone of the Curuçá estuary, north Brazil.
445 Bulletin of Marine Science 80, 739-754
446 Giarrizzo T., Krumme U. (2008) Heterogeneity in intertidal fish fauna assemblages along the
447 world's longest mangrove area in northern Brazil. Journal of Fish Biology 72, 773-779
448 Hammerschlag N., Serafy J.E. (2010) Nocturnal fish utilization of a subtropical mangrove-
449 seagrass ecotone. Marine Ecology 31, 364-374
450 Hindell J.S., Jenkins G.P. (2004) Spatial and temporal variability in the assemblage structure of
451 fishes associated with mangroves (*Avicennia marina*) and intertidal mudflats in temperate
452 Australian embayments. Marine Biology 144, 385-395
453 Hirst D.M. (1962) The geochemistry of modern sediments from the Gulf of Paria—II The
454 location and distribution of trace elements. Geochimica et Cosmochimica Acta 26, 1147-
455 1187
456 Hsieh T.C., Ma K.H., Chao A. (2019) iNEXT: Interpolation and Extrapolation of Species
457 Diversity. R package version 2.0.19
458 Huxham M., Kimani E., Augley J. (2004) Mangrove fish: a comparison of community structure
459 between forested and cleared habitats. Estuarine, Coastal and Shelf Science 60, 637-647

460 Igulu M.M., Nagelkerken I., Dorenbosch M., Grol M.G., Harborne A.R., Kimirei I.A., Mumby
461 P.J., Olds A.D., Mgaya Y.D. (2014) Mangrove habitat use by juvenile reef fish: meta-
462 analysis reveals that tidal regime matters more than biogeographic region. PLoS ONE 9,
463 e114715
464 IMA (2016) State of the marine environment, Trinidad & Tobago. A publication of the Institute
465 of Marine Affairs, Chagaunas, Trinidad and Tobago
466 Jelbart J.E., Ross P.M., Connolly R.M. (2007) Fish assemblages in seagrass beds are influenced
467 by the proximity of mangrove forests. Marine Biology 150, 993-1002
468 Juman R.A., Ramsewak D. (2013) Status of mangrove forests in Trinidad and Tobago, West
469 Indies. Caribbean Journal of Science 47, 291-304
470 Koenig C.C., Coleman F.C., Eklund A.-M., Schull J., Ueland J. (2007) Mangroves as essential
471 nursery habitat for goliath grouper (*Epinephelus itajara*). Bulletin of Marine Science 80,
472 567-585
473 Laegdsgaard P., Johnson C.R. (1995) Mangrove habitats as nurseries: unique assemblages of
474 juvenile fish in subtropical mangroves in eastern Australia. Marine Ecology Progress Series
475 126, 67-81
476 Laegdsgaard P., Johnson C.R. (2001) Why do juvenile fish utilize mangrove habitats. Journal of
477 Experimental Marine Biology and Ecology 257, 229-253
478 Lee S.Y. (2008) Mangrove macrobenthos: assemblages, services, and linkages. Journal of Sea
479 Research 59, 16-29
480 Ley J.A., Halliday I.A. (2007) Diel variation in mangrove fish abundances and trophic guilds of
481 northeastern Australian estuaries with a proposed trophodynamic model. Bulletin of Marine
482 Science 80, 681-720

MacIntyre H.L., Geider R.J., Miller D.C. (1996) Microphytobenthos: the ecological role of the "secret garden" of unvegetated, shallow-water marine habitats. I. Distribution, abundance and primary production. Estuaries 19, 186-201

Mangal E. (2008) Report on commercial fisheries within the Gulf of Paria and the impacts of proposed port development activities on fisheries in the Claxton Bay area. Rapid Environmental Assessments (2003) Limited, Port of Spain, Trinidad

Manson F.J., Loneragan N.R., Harch B.D., Skilleter G.A., Williams L. (2005) A broad-scale analysis of links between coastal fisheries production and mangrove extent: A case-study for northeastern Australia. Fisheries Research 74, 69-85

Marley G., Lawrence A.J., Phillip D.A.T., Hayden B. (2019) Mangrove and mudflat food webs are segregated across four trophic levels, yet connected by highly mobile top predators. Marine Ecology Progress Series 632, 13-25

Mohammed E., Ferreira L., Soomai S., Martin L., Chan A Shing C. (2011) Coastal fisheries of Trinidad and Tobago. In: Salas S., Chuenpagdee R., Charles A., Seijo J.C. (eds) Coastal fisheries of Latin America and the Caribbean. FAO Fisheries and Aquaculture Technical Paper No. 544. Rome, FAO, p 315–356

Mohan J.A., Walther B.D. (2018) Integrating multiple natural tags to link migration patterns and resource partitioning across a subtropical estuarine gradient. Estuaries and Coasts 41, 1806-1820

Nagelkerken I., Van der Velde G. (2002) Do non-estuarine mangroves harbour higher densities of juvenile fish than adjacent shallow-water and coral reef habitats in Curaçao (Netherlands Antilles)? Marine Ecology Progress Series 245, 191-204

505 Nagelkerken I., Blaber S.J.M., Bouillon S., Green P., Haywood M., Kirton L.G., Meynecke J.-
506 O., Pawlik J., Penrose H.M., Sasekumar A. (2008) The habitat function of mangroves for
507 terrestrial and marine fauna: a review. Aquatic Botany 89, 155-185
508 Oksanen J., Kindt R., Legendre P., Stevens M.H.H., Blanchet G., Friendly M., McGlinn D.,
509 Minchin P.R., O'Hara R.B., Simpson G.L., Solymos P., Szoecs E., Wagner H. (2019)
510 Vegan: Community Ecology Package. R package version 2.5-5.
511 Paterson A.W., Whitfield A.K. (2000) Do shallow-water habitats function as refugia for juvenile
512 fishes? Estuarine, Coastal and Shelf Science 51, 359-364
513 Payne N.L., Gillanders B.M. (2009) Assemblages of fish along a mangrove–mudflat gradient in
514 temperate Australia. Marine and Freshwater Research 60, 1-13
515 R-Core-Team (2018) R: A language and environment for statistical computing. Version 3.6.1, R
516 Foundation for Statistical Computing, Vienna, Austria
517 Ramos J.A.A., Barletta M., Dantas D.V., Costa M.F. (2016) Seasonal and spatial ontogenetic
518 movements of Gerreidae in a Brazilian tropical estuarine ecocline and its application for
519 nursery habitat conservation. Journal of Fish Biology 89, 696-712
520 Ray G.L. (2005) Ecological functions of shallow, unvegetated esturaine habitats and potential
521 dredging impacts (with emphasis on Chesapeake Bay). WRAP Technical Notes Collection
522 (ERDC TN-WRAP-05-3), U. S. Army Engineer Research and Development Center,
523 Vicksburg, Mississippi
524 Robertson A.I., Duke N.C. (1987) Mangroves as nursery sites: comparisons of the abundance
525 and species composition of fish and crustaceans in mangroves and other nearshore habitats
526 in tropical Australia. Marine Biology 96, 193-205

527 Robertson A.I., Duke N.C. (1990) Mangrove fish-communities in tropical Queensland, Australia:
528 spatial and temporal patterns in densities, biomass and community structure. Marine Biology
529 104, 369-379
530 Rönnbäck P., Troell M., Kautsky N., Primavera J.H. (1999) Distribution pattern of shrimps and
531 fish among *Avicennia* and *Rhizophora* microhabitats in the Pagbilao mangroves, Philippines.
532 Estuarine, Coastal and Shelf Science 48, 223-234
533 Sheaves M. (2005) Nature and consequences of biological connectivity in mangrove systems.
534 Marine Ecology Progress Series 302, 293-305
535 Sheaves M., Baker R., Nagelkerken I., Connolly R.M. (2015) True value of estuarine and coastal
536 nurseries for fish: incorporating complexity and dynamics. Estuaries and Coasts 38, 401-414
537 Sheaves M., Dingle L., Mattone C. (2016a) Biotic hotspots in mangrove-dominated estuaries:
538 macro-invertebrate aggregation in unvegetated lower intertidal flats. Marine Ecology
539 Progress Series 556, 31-43
540 Sheaves M., Johnston R., Baker R. (2016b) Use of mangroves by fish: new insights from in-
541 forest videos. Marine Ecology Progress Series 549, 167–182
542 Sheridan P. (1997) Benthos of adjacent mangrove, seagrass and non-vegetated habitats in
543 Rookery Bay, Florida, U.S.A. Estuarine, Coastal and Shelf Science 44, 455-469
544 Sheridan P., Hays C. (2003) Are mangroves nursery habitat for transient fishes and decapods?
545 Wetlands 23, 449-458
546 Sheridan P.F. (1992) Comparative habitat utilization by estuarine macrofauna within the
547 mangrove ecosystem of Rookery Bay, Florida. Bulletin of Marine Science 50, 21-39

548 Shervette V.R., Aguirre W.E., Blacio E., Cevallos R., Gonzalez M., Pozo F., Gelwick F. (2007)
549 Fish communities of a disturbed mangrove wetland and an adjacent tidal river in Palmar,
550 Ecuador. Estuarine, Coastal and Shelf Science 72, 115-128
551 Shimps E.L., Rice J.A., Osborne J.A. (2005) Hypoxia tolerance in two juvenile estuary-
552 dependent fishes. Journal of Experimental Marine Biology and Ecology 325, 146-162
553 Silva-Camacho D.D.S., Gomes R.D.S., Santos J.N.S., Araújo F.G. (2017) Distribution of benthic
554 fauna in sediment grains and prop roots of a mangrove channel in south-eastern Brazil.
555 Journal of the Marine Biological Association of the United Kingdom 97, 377-385
556 Smith T.M., Hindell J.S. (2005) Assessing effects of diel period, gear selectivity and predation
557 on patterns of microhabitat use by fish in a mangrove dominated system in SE Australia.
558 Marine Ecology Progress Series 294, 257-270
559 Spach H.L., Santos C., Godefroid R.S., Nardi M., Cunha F. (2004) A study of the fish
560 community structure in a tidal creek. Brazilian Journal of Biology 64, 337-351
561 Tanaka K., Hanamura Y., Chong V.C., Watanabe S., Man A., Kassim F.M., Kodama M.,
562 Ichikawa T. (2011) Stable isotope analysis reveals ontogenetic migration and the importance
563 of a large mangrove estuary as a feeding ground for juvenile John's snapper *Lutjanus johnii*.
564 Fisheries Science 77, 809-816
565 Thayer G.W., Colby D.R., Hettler W.F. (1987) Utilization of the red mangrove prop root habitat
566 by fishes in south Florida. Marine Ecology Progress Series 35, 25-38
567 Tse P., Nip T.H.M., Wong C.K. (2008) Nursery function of mangrove: a comparison with
568 mudflat in terms of fish species composition and fish diet. Estuarine, Coastal and Shelf
569 Science 80, 235-242

570 Valiela I., Bowen J.L., York J.K. (2001) Mangrove forests: one of the world's threatened major
571 tropical environments. AIBS Bulletin 51, 807-815
572 Vaslet A., Bouchon-Navaro Y., Charrier G., Louis M., Bouchon C. (2010) Spatial patterns of
573 mangrove shoreline fish communities in relation with environmental variables in Caribbean
574 lagoons. Estuaries and Coasts 33, 195-210
575 Vilar C.C., Joyeux J.-C., Giarrizzo T., Spach H.L., Vieira J.P., Vaske-Junior T. (2013) Local and
576 regional ecological drivers of fish assemblages in Brazilian estuaries. Marine Ecology
577 Progress Series 485, 181-197
578 Wang M., Huang Z., Shi F., Wang W. (2009) Are vegetated areas of mangroves attractive to
579 juvenile and small fish? The case of Dongzhaigang Bay, Hainan Island, China. Estuarine,
580 Coastal and Shelf Science 85, 208-216
581 Whitfield A. (2017) The role of seagrass meadows, mangrove forests, salt marshes and reed beds
582 as nursery areas and food sources for fishes in estuaries. Reviews in Fish Biology and
583 Fisheries 27, 75-110
584

585 Table 1. PERMANOVA results for the
586 effect of habitat, season and their
587 interaction on the composition of fish
588 communities in three habitats of the Gulf
589 of Paria, Trinidad. Post-hoc pairwise
590 habitat PERMANOVAs also given. **Bold**
591 indicates significance at $p < 0.05$.

Parameters	Df	F	p
Habitat	2	9.32	**<0.001**
Season	1	2.45	**<0.01**
Habitat x Season	2	1.34	0.119
Pairwise tests			
Creeks v Fringe			
Habitat	1	13.02	**<0.001**
Season	1	3.44	**<0.01**
Habitat x Season	1	1.20	0.279
Creeks v Mudflat			
Habitat	1	12.40	**<0.001**
Season	1	2.69	**<0.01**
Habitat x Season	1	0.86	0.609
Fringe v Mudflat			
Habitat	1	1.85	**<0.05**
Season	1	1.87	**<0.05**
Habitat x Season	1	1.73	0.073

592

593

Table 2. SIMPER analysis showing the proportional contributions of species to the dissimilarity in community composition between habitats. Only the most influential species shown.

Habitat comparison	Most influential species (left to right)				Cumulative proportion
Dry season					
Creeks v Fringe	*B. ronchus* 0.31	*D. rhombeus* 0.17	*C. ensiferus* 0.13	*R. saponaceus* 0.08	0.69
Creeks v Mudflat	*B. ronchus* 0.27	*D. rhombeus* 0.15	*C. ensiferus* 0.13	*R. saponaceus* 0.08	0.63
Fringe v Mudflat	*B. ronchus* 0.47	*D. rhombeus* 0.10	*S. colonensis* 0.09	*S. testudineus* 0.07	0.73
Wet Season					
Creeks v Fringe	*B. ronchus* 0.22	*C. ensiferus* 0.20	*S. herzbergii* 0.13	*S. colonensis* 0.11	0.66
Creeks v Mudflat	*C. ensiferus* 0.36	*B. ronchus* 0.09	*S. herzbergii* 0.08	*D. rhombeus* 0.07	0.60
Fringe v Mudflat	*B. ronchus* 0.38	*C. ensiferus* 0.11	*S. colonensis* 0.10	*C. spixii* 0.09	0.68

594

595 Table 3. Summary results of two-way ANOVAs for biodiversity indices, abundance and commercial
596 biomass of fishes between three estuarine habitats of the Gulf of Paria, Trinidad. Post-hoc pairwise t-tests
597 given for significant factors. C = Creeks, F = Fringe, M = Mudflat. **Bold** indicates significance at p <
598 0.05.

Parameters	Two-way ANOVA			Pairwise t-tests (p)		
	Df	F	P	C x F	C x M	F x M
Species richness						
Habitat	2	6.10	**<0.01**	**<0.05**	**<0.05**	**<0.01**
Season	1	0.36	0.548			
Habitat x Season	2	0.69	0.505			
Species diversity						
Habitat	2	3.273	**<0.05**	0.064	0.573	0.064
Season	1	3.453	0.066			
Habitat x Season	2	0.484	0.618			
Juvenile abundance						
Habitat	2	1.61	0.206			
Season	1	0.84	0.363			
Habitat x Season	2	1.31	0.276			
Juvenile species richness						
Habitat	2	6.06	**<0.01**	0.554	**<0.01**	**<0.01**
Season	1	0.35	0.56			
Habitat x Season	2	0.18	0.84			
Commercial biomass						
Habitat	2	6.06	**<0.01**	**<0.01**	0.499	0.081
Season	1	0.35	0.557			
Habitat x Season	2	0.18	0.835			

599

600

601

Table 4. Seasonal variation in physiochemical characteristics of three adjacent fish habitats in the Gulf of Paria, Trinidad. DO=Dissolved O_2.

602

Parameter/ Habitat	Mean±SE (range)	
	Dry	Wet
Salinity		
Creeks	32.1±0.4 (24-37)	24.0±0.5 (18-29)
Fringe	33.5±0.3 (32-34)	25.3±1.0 (22-29)
Mudflat	29.4±0.3 (28-30)	26.5±0.4 (25-28)
Temperature (°C)		
Creeks	27.2±0.2 (25-30)	27.5±0.2 (25-29)
Fringe	27.1±0.2 (26-29)	27.9±0.3 (27-30)
Mudflat	27.3±0.1 (27-28)	27.7±0.2 (27-28)
DO (mg l^{-1})		
Creeks	2.9±0.2 (0.4-5.3)	2.9±0.2 (1.1-5.4)
Fringe	5.1±0.2 (4.3-6.0)	4.7±0.6 (3.3-9.1)
Mudflat	5.1±0.3 (4.0-5.7)	6.4±0.6 (4.8-8.6)
Turbidity (cm)		
Creeks	74±5 (1-160)	58±5 (15-140)
Fringe	77±8 (50-123)	51±4 (30-70)
Mudflat	46±3 (40-60)	57±15.(25-120)

603

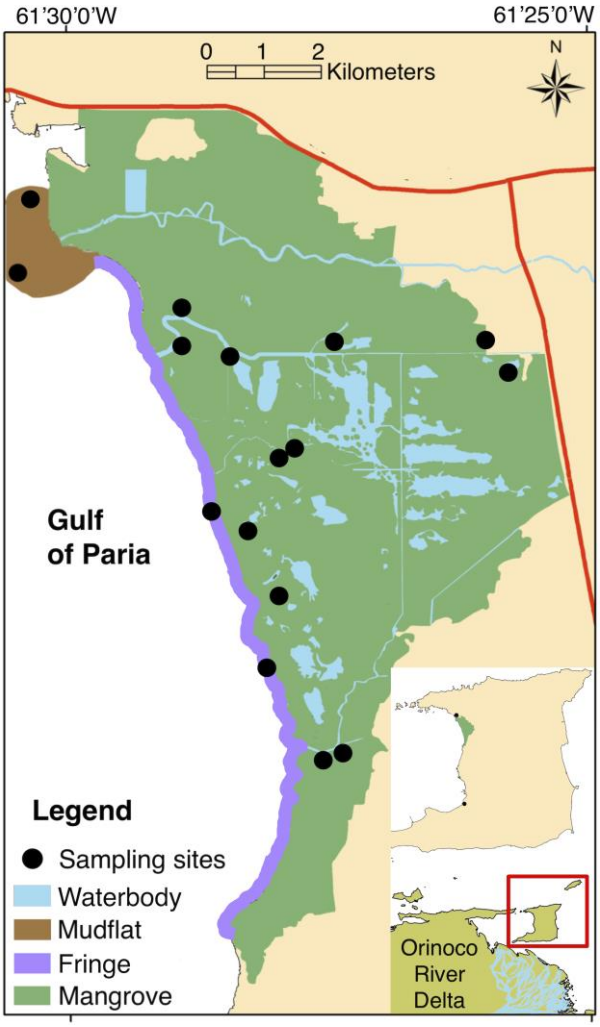


Fig. 1. Survey sites in the Caroni Swamp mangrove and adjacent mudflat habitats, Trinidad, Gulf of Paria.

605

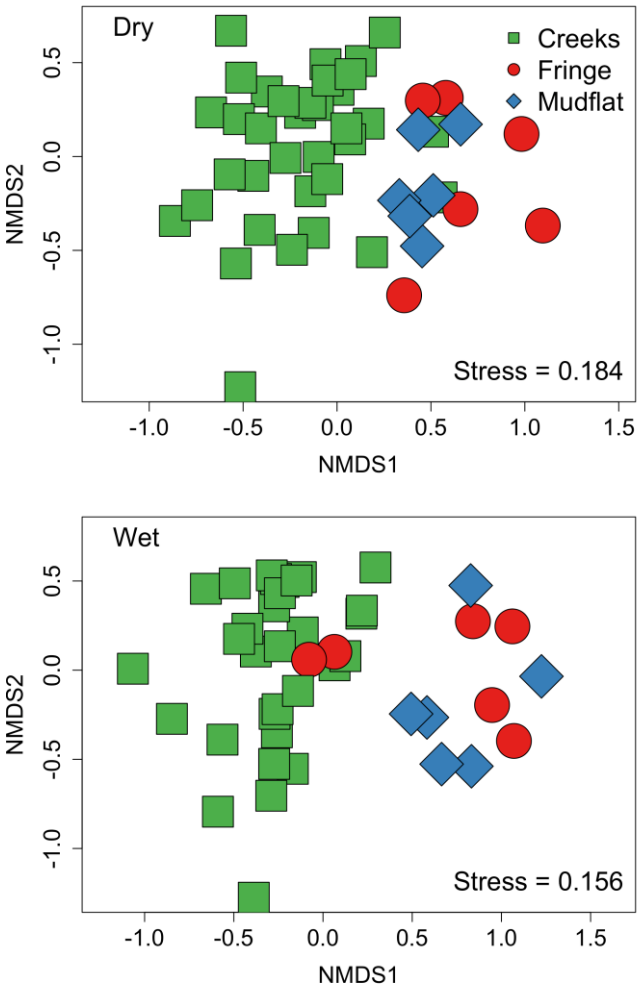
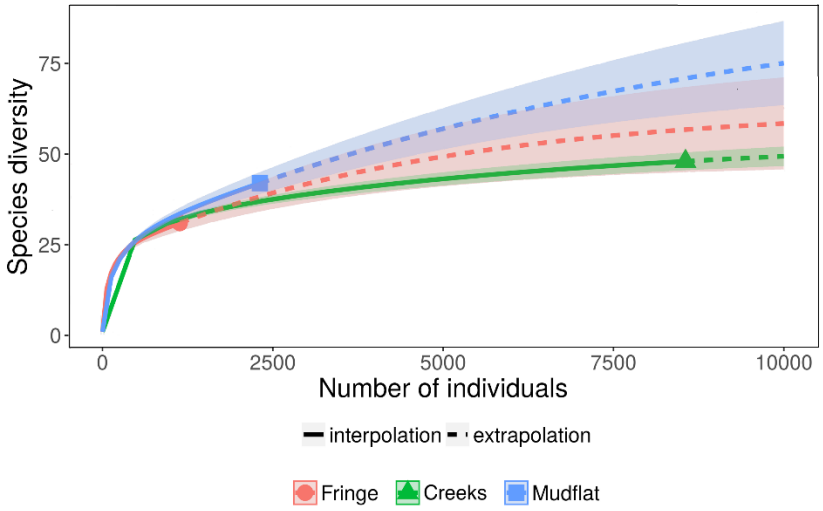


Fig. 2. NMDS plots of species composition (by abundance) of season specific fish communities in three habitats of the Gulf of Paria, Trinidad. Dissimilarity based on a Bray-Curtis matrix. Dimensions = 3.

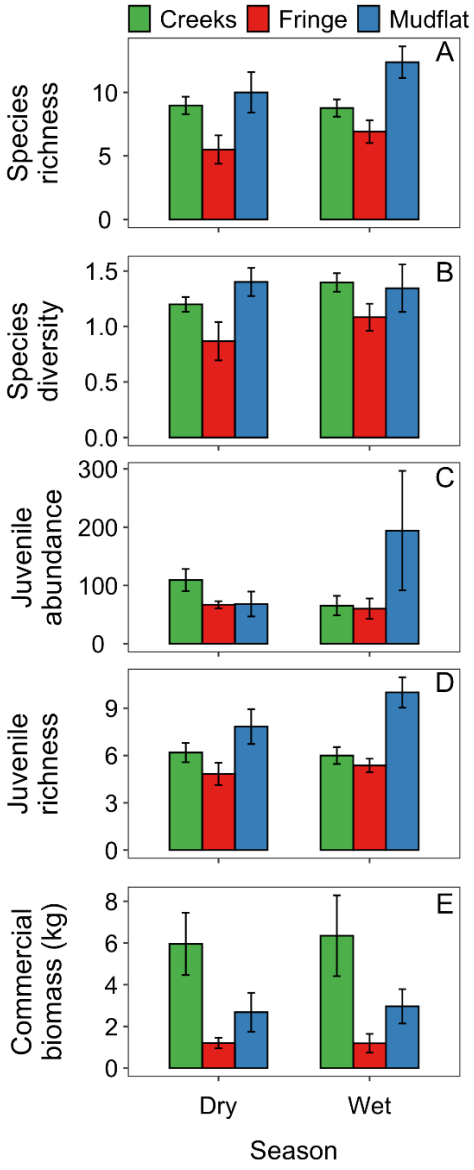
606



607

608 Fig. 3. Species accumulation curves for the accumulation of new species with number of individuals
609 sampled and individual-based rarefaction and extrapolation to 10,000 individuals sampled (±1 SD).

610



611

612 Fig. 4. Mean (±SE) biodiversity indices standardised per catch: A) species richness; B) species diversity
613 (Shannon Wiener index); C) juvenile fish abundance; D) juvenile species richness; E) commercial fish
614 biomass in habitats of the Gulf of Paria, Trinidad.
615